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Baboons' hand preference resist to spatial factors for a communicative gesture but not for a simple manipulative action

Marie Bourjade[1], Hélène Meunier[2], Catherine Blois-Heulin[3] & Jacques Vauclair[1]

[1] Research Centre in the Psychology of Cognition, Language and Emotion, Aix-Marseille University, Aix-en-Provence, France

[2] Primatology Centre of Strasbourg University, Fort Foch, 67207 Niederhausbergen, France

[3] UMR 6552 Ethos « Ethologie Animale et Humaine », Université de Rennes 1 - CNRS, Station biologique, Paimpont, France

Corresponding author:

Marie Bourjade

Research Center in the Psychology of Cognition, Language and Emotion, PsyCLE, Aix-Marseille University, 29 av. Schuman, 13621 Aix-en-Provence Cedex 1, France

marie.bourjade@univ-amu.fr, marie.bourjade@gmail.com

+033 6 12 41 50 88

Olive baboons (*Papio anubis*) do acquire and use intentional requesting gestures in experimental contexts. Individual's hand preference for these gestures is consistent with that observed for typical communicative gestures, but not for manipulative actions. Here, we examine whether the strength of hand preference may also be a good marker of hemispheric specialization for communicative gestures, hence differing from the strength of hand preference for manipulative actions. We compared the consistency of individuals' hand preference with regard to the variation in space of either (i) a communicative partner or (ii) a food item to grasp using a controlled set-up. We report more consistent hand preference for communicative gestures than for grasping actions. Established hand preference in the midline was stronger for gesturing than for grasping and allowed to predict the consistency of hand preference across positions. We found no significant relation between the direction of hand preference and the task.

Key words: Handedness, Laterality, Language, Gesture, Hand preference, Olive baboon

Handedness is by far the most overwhelming manifestation of behavioral asymmetry in humans. A right-hand preference is shown by approximately ninety percent of humans (Annett, 1985; Knecht et al., 2000a), and this population-level bias is considered universal because of its existence across all modern cultures (Coren & Porac, 1977; Raymond & Pontier, 2004) and over the course of human evolution (Cashmore, Uomini, & Chapelain, 2008; Faurie & Raymond, 2004; Uomini, 2009). From a neurofunctional viewpoint, handedness is also one robust manifestation of hemispheric specialization, the other one being language lateralization (Hopkins & Vauclair, 2012). Indeed, right-handers are left-hemisphere dominant for hand functions and most humans are also left hemisphere dominant for language functions. Both features have hence been argued to evolve concomitantly during the course of human evolution (Crow, 2004; Ettlinger, 1988; Waren, 1980).

However, recent studies have emphasized that handedness would actually be only a poor predictor of hemispheric dominance for language. First, a majority of left-handers are also left hemisphere dominant for language in humans (Knecht et al., 2000b; Khedr, Hamed, Said, & Basahi, 2002). Moreover, asymmetries in the use of limbs are not specific to humans but are widespread in vertebrates instead (Hopkins, 2007; Rogers & Andrew, 2002; Vallortigara, Rogers, & Bisazza, 1999). It has hence been proposed that handedness predated language (Corballis, Badzakova-Trajkov, & Häberling, 2012; Forrester, Quaresmini, Leavens, Mareschal, & Thomas, 2013) and there is still considerable debate about whether left-hemisphere dominance for language was inherited from hemispheric specialization for its motor components (Greenfield 1991; Forrester et al., 2013) or rather its communicative components (Vauclair, 2004). In that respect, communicative gestures that imply both motor and communicative hand functions have been of particular interest in the recent years. Children point more frequently with their right hand (Bates, O'Connell, Vaid, Sledge, & Oakes, 1986; Cochet & Vauclair, 2010), even if they are left-handers or ambidextrous for

manipulating objects otherwise (Vauclair & Imbault, 2009). Interestingly hand preference may be more pronounced for communicative gestures such as pointing than for object manipulation, and both types of hand preference are usually poorly correlated in human infants (Cochet & Vauclair, 2010; Jacquet, Esseily, Rider, & Fagard, 2012; Vauclair & Imbault, 2009). This has led some to hypothesize that hand preference for communicative gestures may be a better marker of hemispheric specialization for language than handedness (Cochet & Vauclair, 2010; Kimura, 1993; Vauclair, 2004).

Further support for this hypothesis comes from comparative work conducted with non-human primates. Several studies have for example found right-sided asymmetries at the population level in both the chimpanzee (Hopkins et al., 2005; Meguerditchian, Vauclair, & Hopkins, 2010) and the baboon (Meguerditchian, Molesti, & Vauclair, 2011b; Meguerditchian & Vauclair, 2006) for a range of manual tasks, including complex (i.e., bimanual) manipulations and communicative gestures. As it is the case for children (Esseily, Jacquet, & Fagard, 2011; Jacquet et al., 2012; Vauclair & Imbault, 2009), the population-level right biases found in both species were stronger for communicative gestures than for object-directed manual actions, (e.g. baboons: Meguerditchian & Vauclair, 2009; chimpanzees: Hopkins et al., 2005; Meguerditchian et al., 2010). Consequently, a similar pattern of hand preference can be observed in human and in some non-human primates (see also Meunier, Vauclair, & Fagard, 2012b; Meunier et al., this issue), albeit in different proportions. Taken together, these data suggest that the left-hemisphere dominance in linguistic functioning is not modality-specific and may have deep phylogenetic origins (Corballis et al., 2012; Meguerditchian, Cochet, & Vauclair, 2011a; Vauclair, 2004).

In two studies conducted in our laboratory, we found that baboons were able to request food intentionally from a human partner using either pointing (Meunier, Prieur, & Vauclair, 2012a) or food-begging gestures (Bourjade, Meguerditchian, Maille, & Vauclair, submitted).

While both gestures are communicative, presumed difference exists since pointing, but not begging, requires attracting the attention of a human towards an external distinct target and has been suggested to involve higher cognitive demands in monkeys (e.g. Hattori, Kuroshima, & Fujita, 2010). Interestingly, the pattern of laterality for pointing was similar in baboons and human infants (Meunier et al., 2012b), while it has not been investigated so far for food-begging. As regards food-begging, baboons were shown to keep their hand preference consistent with a typical communicative gesture (i.e., hand slapping), but not with object-directed manual actions (Meguerditchian & Vauclair, 2009). The authors hypothesized that baboons' communicative gestures, as regards the direction and consistency of hand preference, may rely on a specific left-lateralized cerebral system that would be independent from the system controlling purely manipulative actions (Meguerditchian et al., 2011a). However, overall direction of hand preference may not be the only aspect that has neuropsychological significance. Handedness is commonly measured as a discrete variable based on the predominant use of the right or the left hand, or equivalent use of both hands. In contrast, many have suggested that measuring handedness on a continuous scale accounted for both the direction and the strength of hand preference, with the latter also being a good marker of brain specialization (e.g. Bishop, Ross, Daniels, & Bright, 1996; Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997; Khedr et al., 2002; Vallortigara et al., 1999). Neurofunctional evidence supports this claim since the strength and direction of handedness seem to be coded separately in the human brain (Dassonville et al., 1997). Likewise, it could be alternately hypothesized that the strength of hand preference for communicative gestures, defined as the proportion of same-hand use for a given gesture, may be a good marker of hemispheric specialization for communicative hand functions in baboons, hence differing from the strength of hand preference for manipulative actions.

In this contribution, we examine these two hypotheses alternately using a standardized measure for quantifying consistency of hand preference as a tool towards validation (i.e., QHP task, Bishop et al., 1996). The initial task developed in humans was to pick up playing cards. The use of the non-preferred hand was encouraged by varying the spatial position of the cards in relation to the body midline. The prediction was that switching hand across positions indicated weaker preferences than keeping hand consistent across positions. Adaptations of this task for children (Esseily et al., 2011; Jacquet et al., 2012) and non-human primates (Chapelain et al., 2012; Meunier, Blois-Heulin, & Vauclair, 2011; Meunier et al., 2012b; Meunier et al., this issue) have proved recently successful in highlighting the influence of situational factors on handedness for reaching actions.

Our aim of adapting this paradigm here was to use the sensitivity to situational factors as a means of measuring the robustness of hand preference of subjects predefined as right-handed, left-handed, ambiguously-handed, but also those established as exclusively-handed and non-exclusively handed irrespective of the direction of laterality. The rationale was then to determine the consistency of hand preference across spatial positions (herein: *consistency* of hand preference) in two different tasks, taking established hand preference (i.e., both in direction and strength) in the central position as a reference. We built on previously published data reporting hand preference for grasping in baboons (Meunier et al., 2011) to compare with novel data reporting hand preference for food-begging measured on same individuals within the same experimental setting. In order to portray the differential lateralization of communicative and non-communicative hand functions, we examined the *consistency* across positions of both the *direction* and the *strength* of individuals' hand preference with regards to the variation in space of (i) a communicative partner (i.e., food-begging) and (ii) a food item to grasp (i.e., grasping).

Based on previously published research reporting stronger biases for communicative gestures than for grasping actions at the population level (Meguerditchian & Vauclair, 2009; Meunier et al., 2011; Meunier et al., 2012b), we expected hand preference to be more consistent across positions in the communicative than in the non-communicative context. Additionally, if the cerebral system controlling for communicative gestures differs from the system controlling manipulative actions on the basis of the *direction but not strength* of hand preference, we would expect more established right-handers than left-handers in the central position for food-begging than for grasping, and the direction of the established preference to predict the propensity to switch from preferred to non preferred hand. Alternately, if the two systems differ on the basis of the *strength but not direction* of hand preference, we would expect baboons to show stronger established hand preference for food-begging than for grasping, and the strength of the established preference to predict the propensity to switch from preferred to non preferred hand.

METHODS

Animals

The experiments took place in the Primate Station of the *Centre National de la Recherche Scientifique*, Rousset, France. Initially, 42 olive baboons (*Papio anubis*) were presented with the grasping task between September and December 2009 (see Meunier et al., 2011 for details). Two years later, 13 out of these subjects were presented with a food-begging task. These subjects had previously learnt to request food by extending an arm through the cage in former experiments (e.g. Bourjade et al., submitted; Meunier et al., 2012a). Only the data for these 13 subjects that have completed the two tasks are presented here. Subjects were five females and eight males, all adult. All lived in social groups and were housed either in

outdoor parks or large cages with free access to an indoor shelter. Water was available *ad libitum* and subjects were never deprived of food or water during testing. All subjects had been tested in their outdoor area, and only females were partly isolated from dominant individuals (i.e., that were kept inside) during testing for the food-begging task. All procedures complied with the current French laws and the European directive 86/609/CEE.

Experimental procedure

For the two tasks, the experimental set-up was an adaptation of the Bishop's QHP task initially developed to test pre-defined human right-handers for their degree of hand preference (Bishop et al., 1996). In the original task seven picture cards were placed on a semi-circle, each positioned 30 degrees apart from one another, in front of- and within the reach of the participant. Participants stood in front of the template and had to pick up specific cards one by one to put them in a box located in front of them. Hand preference was sampled by recording the hand used to pick up each card. This task has been thereafter adapted to non-human primates in a very comparable set-up (Chapelain et al., 2012; Meunier et al., 2011; Meunier et al, this issue). We provide a brief description of the experimental set-up here. Full details of the methods and procedures are available elsewhere (Chapelain et al., 2012; Meunier et al., 2011; Meunier et al., 2012b).

We used a similar apparatus for both tasks. Subjects sat down a concrete block fixed perpendicularly to the mesh inside the cage at about 90 cm from the ground. There was a 10x60 cm hole in the wire-mesh that allowed the subject to pass its arms through. Two video cameras were placed 2 m in front of the cage on both sides of the experimenter with an angle of 45° to the subject's midline. For the food-begging task only, subjects were additionally provided with a bottle hung inside the cage, filled with diluted fruit juice to prevent them

orienting their body towards the experimenter, particularly when she positioned laterally (see supplementary material).

For the grasping task, the playing card was replaced by a food item that was randomly and successively placed at one of the seven positions placed at 30° from each other on a semi-circle drawn on a tray fixed outside of the wire-mesh (Figure 1a). Only one item, i.e., a raisin, was placed at a time and the experimenter randomly used her right or left hand to place it. Hand preference had been sampled by recording the hand used by subjects to grasp the raisin.

For the food-begging task, the playing card was replaced by the experimenter herself holding a piece of food in one hand. The experimenter randomly and successively positioned herself at one of the positions placed at 30° from each other on a 1 m radius semi-circle drawn on a textile sheet lying on the ground in front of the subject's cage (Figure 1b). The experimenter approached the apparatus from one meter away, always starting from the midline and heading towards the position to be tested. The experimenter randomly used her right or left hand to hold the piece of food, i.e., a 2 cm piece of banana. Hand preference was sampled by recording the hand used by subjects to beg for food.

Note that for the food-begging task five positions only could be reliably scored. The two most extreme positions that had not been tested for food-begging were therefore not considered anymore in the present paper for grasping. Consequently, the five remaining positions (i.e., corresponding to positions 2 to 6 in Meunier et al., 2011) were: extreme left (LL), left (L), central (C), right (R) and extreme right (RR) from the left to the right of the subject (Figure 1). For each task, the order of presentation of the positions was randomized beforehand and then, the same order was presented for all subjects. The trials were scored as valid or invalid on subsequent video analysis. A valid trial was considered when the subject sat in front of the setup aligned with the middle of the apparatus. Video material was coded by

two independent observers whose one was naïve to the experimental procedure. We only kept the trials that have been scored as valid by the two observers for further analysis. Thus, subjects reached 20 to 60 valid trials per position for grasping and 8 to 35 valid trials per position for food-begging.

Data analysis

The *direction* of hand preference was determined with binomial tests on the number of right and left responses of each individual for each task and each position to evaluate departure from chance level and categorize individuals as right-, left- or ambiguously-handed accordingly. Handedness Index (HI) was calculated for each task and position by subtracting the number of left-handed responses from the number of right-handed responses and then dividing by the total number of responses (Hopkins, 1999). HI ranged from -1.0 to +1.0 with positive values indicating right-hand bias and negative values left-hand bias. The *strength* of hand preference was assessed thanks to the absolute value of HI (ABSHI) ranging from 0 to 1. Subjects displaying a significant bias in any position were categorized as *lateralized* for these positions. Subjects with ABSHI = 1 were categorized as *exclusively-handed*, the other subjects as *non-exclusively-handed.* When referring to individuals as right-, left-, exclusively- or non-exclusively-handed or as lateralized, we referred to individual's established hand preference in the central position for each task.

We applied generalized linear mixed models (GLMM) to our data in order to investigate the influence of situational factors as a function of the task. Several models were fitted with the proportion of right-handed over total responses of each individual in each position and each task as dependent variable (see summary of models fitted as supplementary material). Depending on the models, fixed effects were alternately or simultaneously (i) the

position, (ii) the task, (iii) the subject's sex and (iv) the interactions between them. The positive correlation amongst observations of the same individual was taken into consideration by adding the individual or the interaction between individual and position as random effect, which allowed each individual to respond differently to positions (Brown & Prescott, 2006). The family chosen for the dependent variable in the models was Binomial with a Logit link function; model selection was based on the Akaike Information Criteria (AIC; Onyango, 2009).

As the rationale of the QHP task was to foster subjects on to switch from their preferred to non-preferred hand in the contralateral hemispace, we counted the number of subjects that switched hand at 30 and 60 degrees in the non-preferred contralateral hemispace. As almost all subjects, but two, that switched hand did so at 30° in the contralateral hemispace, we considered this angle only for statistical analysis. Non-parametric statistics (Siegel & Castellan, 1988) were performed on such categorical data, as well as ABSHI and individual's mean HI for each task and each position. All tests were performed with R 2.10.1 software (http://cran.r-project.org) with level of significance set at 0.05.

RESULTS

Comparison between tasks on the basis of the direction of hand preference

The baboons did not display similar patterns of direction of hand preference for food-begging and for grasping (i.e. best fitting model, AIC = 690.6; Table 1). There was a significant effect of the task on the proportion of right-handed responses (Wald Test, $z = -4.23$, $p < 0.001$), and a significant interaction between task and position (Figure 2). It means that the direction of hand preference varied as a function of both task and position, with baboons being more right-handed for food-begging than for grasping in the position LL (Wald test, $z = -9.92$, $p < 0.001$)

and position L (Wald test, $z = -8.02$, $p < 0.001$), and more right-handed for grasping than for food-begging in the position R (Wald test, $z = 11.54$, $p < 0.001$) and position RR (Wald test, $z = 10.83$, $p < 0.001$). Irrespective of the task, baboons were overall more right-handed than left-handed for position R (Wald test, $z = 2.23$, $p = 0.026$), but not for positions RR (Wald test, $z = 0.71$, $p = 0.473$), L (Wald test, $z = -0.81$, $p = 0.417$) and LL (Wald test, $z = -0.55$, $p = 0.583$).

Each baboon did not keep similar hand preference for food-begging and for grasping based on handedness index (HI). HI did not correlate between tasks for all positions (Spearman correlation coefficients, position LL: $r = 0.17$, p 0.573; position L: $r = 0.21$, $p = 0.483$; position C: $r = 0.39$, $p = 0.184$; position RR: $r = 0.44$, $p = 0.127$), except position R (Spearman correlation coefficient, $r = 0.58$, $p = 0.037$). The average HI across all positions for each individual did not correlate between tasks (Spearman correlation coefficient, $r = 0.34$, $p = 0.252$).

Comparison between tasks on the basis of the strength of hand preference

The baboons did not display similar patterns of strength of hand preference for food-begging and for grasping when considering ABSHI across positions (Figure 4). The strength of hand preference was affected overall by the position of the item to grasp (Friedman analysis of variance, $F(4) = 29.97$, $p < 0.001$) but not by the position of the experimenter whom to beg from (Friedman analysis of variance, $F(4) = 1.55$, $p = 0.834$). Direct comparisons between the two tasks in each position reveal that the strength of hand preference was significantly higher for food-begging than for grasping in the central position (one-sample permutation test, $t = 2.01$, $p = 0.042$), while it was significantly lower in the position LL (one-sample permutation test, $t = -2.02$, $p = 0.039$). There was no significant difference in the strength of hand

preference between the two tasks for the positions RR, R and L (one-sample permutation tests, $p > 0.05$ in all cases).

This result is gaining support by the fact that the consistency of hand preference across positions also varied as a function of the task. Based on established hand preference in the central position (Tables 2 & 3), lateralized baboons were more likely to switch from preferred to non-preferred hand in the contralateral space for grasping than for food-begging, irrespective of the direction of laterality (Fisher exact probabilities test, $p = 0.002$).

Discriminatory power of direction versus strength of hand preference

For hand preference established in the central position (Tables 2 & 3), we found no significant difference between the number of right-handed and left-handed baboons as a function of the task (Fisher exact probabilities test, $p = 1$), while we found more exclusively-handed baboons than non-exclusively handed baboons for food-begging than for grasping (Fisher exact probabilities test, $p = 0.002$). Eight subjects out of 13 displayed exclusive hand preference for food-begging whereas no subject displayed exclusive hand preference for grasping in the midline.

The strength of hand preference established in the central position for food-begging (i.e., as exclusively- or non-exclusively-handed baboons) allowed predicting the propensity of individuals to switch from preferred to non-preferred hand in the contralateral hemispace (Fisher exact probabilities test, $p = 0.022$, Table 3). All the eight baboons that had exclusive hand preference for food-begging in the central position kept their preferred hand in the contralateral hemispace, while the two lateralized baboons that had non-exclusive hand preference in the central position switched to non-preferred hand at 30 degrees in the contralateral hemispace. However, the direction of hand preference established in the central

position, did not allow predicting the propensity of individuals to switch from preferred to non-preferred hand in the contralateral hemispace for grasping (Fisher exact probabilities test, $p = 1$, Table 2), nor for food-begging (Fisher exact probabilities test, $p = 0.444$, Table 3).

DISCUSSION

Three main points are worth noting in the present contribution. First, the differential distribution of hand biases for gesturing toward a partner and for grasping an item corroborates previous results obtained in baboons and other species (Meunier et al., 2012b; Meunier et al., this issue) and stresses that these two manual actions seem not to be processed similarly by the brain. Second, this investigation sheds light on the relative influence of the strength of hand preference in distinguishing communicative from non-communicative tasks in an old-world-monkey. Third, these results clearly state that situational factors have little influence on hand preference for gesturing in a communicative context, as reported in macaques (Meunier et al., this issue), chimpanzees (Hopkins & Wesley, 2002) and human infants (Jacquet et al., 2012).

Influence of the nature of the task on hand preference

Our examination that compared hand use for grasping and for food-begging pointed out differential use of the right hand according to situational factors. Baboons hardly ever used their right hand to grasp a raisin situated on their left side, but used more often their right hand for begging from an experimenter located at same positions. Conversely, subjects used their right hand more often to grasp a raisin situated on their right than to beg for food from an experimenter situated on their right. These findings indicate that the position in space largely

influences hand use for grasping but not hand use for requesting food from a partner. This is supported by the fact that baboons did not keep the direction of their hand preference consistent between tasks. Handedness indices measured on same individuals for the two tasks were very poorly correlated, except for the position R. The reason why these two indices correlate for this position only is not straightforward. As observed in humans for different activities (Steenhuis, 1999), left-handed baboons may be more likely to switch hand for gesturing in the contralateral hemispace than right-handed baboons, but it does not explain why a similar trend was not observed for the extreme right position.

The tasks also elicited different patterns of strength of hand preference across positions. At the group level, the strength of hand preference for grasping a raisin in the extreme rightward and leftward positions was high, whereas it was low in the more central positions. Contrarily, the measures of strength for food-begging did not vary across positions**.** In other words, situational factors do not affect the strength of hand preference for food-begging while they affect the strength of hand preference for grasping. At the individual level, this task-related effect underlies two opposite patterns of occurrences of hand switch. In the contralateral hemispace subjects kept their preferred hand for begging for food, but switched to non-preferred hand for grasping, irrespective of the direction of hand preference. Together, these findings illustrate that the more pronounced biases for communicative gestures than for object manipulation recorded at the population level (Meguerditchian & Vauclair, 2009; Meunier et al., 2011; Meunier et al., 2012b) are underpinned by stronger hand preference at the individual level for communicative gestures than for grasping.

Such a differential effect of situational factors on hand preference is in line with the few available studies that have compared handedness for different manual tasks and/or species using the QHP task. For instance, it had been found that the direction of hand preference was strongly affected by the position of an item to grasp in mangabeys and

Campbell's monkeys (Chapelain et al., 2012). In a comparative work, Meunier and colleagues (2012b; this issue) highlighted convergent distributions of hand biases in macaques, baboons and human infants, with patterns very similar to ours. Human infants have otherwise been shown to use more their right hand to point to objects than to grasp them and to be more willing to use their right hand in the contralateral left hemispace for pointing than for grasping (Jacquet et al., 2012).These collective data, all gathered with a similar experimental set-up (the QHP task), support the hypothesis that functional asymmetries for gesturing in a communicative context and for grasping may develop quite independently in humans and non-human primates, perhaps due to differential constraints on their expression.

Significance of the direction and the strength of hand preference

Both right-handed and left-handed baboons for grasping switched from preferred to non-preferred hand in the contralateral hemispace, while both right-handed and left-handed baboons for begging kept their preferred hand in the contralateral hemispace. This suggests that the direction of hand preference does not discriminate between the tasks, at least in our sample. Our data show however that the strength of hand preference in the midline may be a good predictor of the consistency of hand preference across positions, at least for food-begging. Three results are worth noting. First, the strength of baboons' hand preference was higher for food-begging than for grasping in the midline. Second, none of the subjects had exclusive preferences for one hand in the grasping task, whereas almost all of them had exclusive preferences for one hand in the food-begging task. Third, the baboons with established exclusive preferences for food-begging in the midline were less likely to switch hand across positions than the baboons with established non-exclusive preferences. Therefore,

baboons' hand preference seems to differ between tasks on the basis of the strength of hand preference, rather than the direction.

These results are gaining support from neuroimaging evidence in humans of a continuous relation between the strength of handedness and functional activation of the motor cortex (Dassonville et al., 1997). These authors found both right and left-handers having similar contralateral activation of the motor cortex concomitant to the use of the dominant hand. However, the strength of hand preference correlated negatively with the cerebral activation ipsilateral to the dominant hand. It means that activation in the motor cortex is more lateralized with increasing strength of handedness in both right-handers and left-handers. Additional research is needed to confirm whether the strength of hand preference might have similar neurofunctional significance in non-human primates.

Although human infants (Cochet & Vauclair, 2010; Esseily et al., 2011; Jacquet et al., 2012; Vauclair & Imbault, 2009), like chimpanzees and baboons (Hopkins et al., 2005; Meguerditchian et al., 2010; Meguerditchian & Vauclair, 2009), have been reported to be more right-handed for gesturing than for manipulating objects, it is worth noting that no population-level bias emerged in the present data. It is possible that our sample size was too small to detect any population-level bias for food-begging. As proposed above, it could alternately be that the strength of hand preference for communicative gestures may be a better marker of hemispheric specialization than the direction of hand preference for the use of learnt gestures in baboons. As the direction of hand preference may be partly determined by epigenetic constraints (Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009; Vallortigara et al., 1999), it is possible that brain specialization for these gestures may have been constrained by individual learning history, leading to differential lateralization at the population level. It would explain why the population right-sided bias was found lower for

food-begging than for typical gestures in baboons, though both indices correlate nevertheless (Meguerditchian & Vauclair, 2009).

Conclusion

Baboons show stronger hand preference for communicative gestures than for manipulative action irrespective of the direction of laterality. Hand preference for gesturing is little influenced by situational factors and this consistency can be predicted by the strength of hand preference in the midline. Based on these findings, we suggest that behavioral asymmetries for gestural communication and for manipulative actions in baboons rely on independent brain processes that differ with the strength of hand preference, possibly reflecting differential degrees of lateralization in brain activation. Additional research is needed to evaluate whether the apparent behavioral continuity that exists between baboons, chimpanzees and humans with respect to manual asymmetries has neurological underpinnings.

NOTES

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Table 1. Summary of models fitted with the proportion of right-handed responses as dependent variable. Interactions between two effects are represented by colons. Bold characters indicate the best fitting model, which significantly differed from the null model fitted without fixed effects (Chi-square tests for the log-likelihood ratios, $p < 0.001$).

Dependent variable	Model	Fixed effects	Random effects	AIC
Proportion of right-handed responses				
	1	none	individual	4292
	2	task	individual	4283
	3	task	individual:position	1676
	4	position	individual	1717
	5	position	individual:position	1659
	6	task, position, task:position	individual	820
	7	**task, position, task:position**	**individual:position**	**691**
	8	task, sex, position, task:sex	individual	1624
	9	task, sex, position, task:sex	individual:position	1690

Table 2. Raw data for each individual tested in the grasping task

Individual	Sex	LL				L				C				R				RR			
		LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI
Anelka	M	**50**	10	<0.001	-0.67	36	24	0.155	-0.20	19	**41**	0.006	0.37	1	**59**	<0.001	0.97	0	**60**	**<0.001**	**1.00**
Katy	F	**60**	0	<0.001	**-1.00**	**53**	7	<0.001	-0.77	17	**43**	0.001	0.43	2	**58**	<0.001	0.93	1	**59**	**<0.001**	0.97
Marius	M	**60**	0	<0.001	**-1.00**	**60**	0	<0.001	**-1.00**	29	31	0.897	0.03	1	**59**	<0.001	0.97	0	**60**	**<0.001**	**1.00**
Momo	M	**60**	0	<0.001	**-1.00**	**60**	0	<0.001	**-1.00**	**54**	6	<0.001	-0.80	0	**60**	<0.001	**1.00**	0	**60**	**<0.001**	**1.00**
Oscar	M	**59**	1	<0.001	-0.97	**60**	0	<0.001	**-1.00**	**50**	10	<0.001	-0.67	1	**59**	<0.001	0.97	0	**60**	**<0.001**	**1.00**
Perfide	F	**60**	0	<0.001	**-1.00**	**57**	3	<0.001	-0.90	37	23	0.092	-0.23	12	**48**	<0.001	0.60	0	**60**	**<0.001**	**1.00**
Prise	F	**55**	5	<0.001	-0.83	**46**	14	<0.001	-0.53	28	32	0.699	0.07	4	**56**	<0.001	0.87	4	**56**	**<0.001**	0.87
Rodolphe	M	**60**	0	<0.001	**-1.00**	**60**	0	<0.001	**-1.00**	**57**	3	<0.001	-0.90	5	**55**	<0.001	0.83	0	**60**	**<0.001**	**1.00**
Sestarde	F	**18**	2	<0.001	-0.80	9	11	0.412	0.10	2	**18**	<0.001	0.80	0	**20**	<0.001	**1.00**	0	**20**	**<0.001**	**1.00**
Toti	M	**60**	0	<0.001	**-1.00**	**60**	0	<0.001	**-1.00**	37	23	0.092	-0.23	1	**59**	<0.001	0.97	0	**60**	**<0.001**	**1.00**
Tulie	F	**60**	0	<0.001	**-1.00**	**57**	3	<0.001	-0.90	38	22	0.052	-0.27	10	**50**	<0.001	0.67	1	**59**	**<0.001**	0.97
Ubu	M	**60**	0	<0.001	**-1.00**	**60**	0	<0.001	**-1.00**	**49**	11	<0.001	-0.63	3	**57**	<0.001	0.90	2	**58**	**<0.001**	0.93
Uranus	M	**60**	0	<0.001	**-1.00**	**51**	9	<0.001	-0.70	32	28	0.698	-0.07	2	**58**	<0.001	0.93	0	**60**	**<0.001**	**1.00**
Handedness category																					
LH-RH		13	0			11	0			4	3			0	13			0	13		
LAT				13				11				7				13				13	
EXC					9				6				0				2				9

Sex: *M* male, *F* female. Main columns: *LH* number of left-handed responses, *RH* number of right-handed responses, *B test* p-value of the binomial test performed on the number of right-handed and left-handed responses (when the test is significant the higher value is in bold), *HI* handedness index (bold characters indicate exclusive hand preference). Handedness category: *LH-RH* number of left-handed and right-handed baboons, *LAT* number of lateralized baboons irrespective of the direction of laterality, *EXC* number of exclusive right-handed and left-handed baboons (HI = 1 or HI = -1).

Table 3. Raw data for each individual tested in the food-begging task

Individual	Sex	LL				L				C				R				RR			
		LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI
Anelka	M	0	**17**	<0.001	**1.00**	0	**18**	<0.001	**1.00**	0	**20**	<0.001	**1.00**	0	**20**	<0.001	**1.00**	0	**20**	<0.001	**1.00**
Katy	F	0	**18**	<0.001	**1.00**	1	**19**	<0.001	0.90	0	**20**	<0.001	**1.00**	0	**19**	<0.001	**1.00**	0	**14**	<0.001	**1.00**
Marius	M	0	**17**	<0.001	**1.00**	0	**19**	<0.001	**1.00**	0	**20**	<0.001	**1.00**	0	**20**	<0.001	**1.00**	0	**16**	<0.001	**1.00**
Momo	M	5	**14**	0.032	0.47	2	**17**	<0.001	0.79	0	**19**	<0.001	**1.00**	0	**20**	<0.001	**1.00**	0	**15**	<0.001	**1.00**
Oscar	M	11	4	0.059	-0.47	**16**	2	0.001	-0.78	**13**	4	0.025	-0.53	11	7	0.240	-0.22	**14**	1	<0.001	-0.87
Perfide	F	**19**	1	<0.001	-0.90	**14**	5	0.032	-0.47	10	7	0.315	-0.18	5	10	0.151	0.33	4	7	0.274	0.27
Prise	F	**19**	0	<0.001	**-1.00**	**21**	0	<0.001	**-1.00**	**21**	0	<0.001	**-1.00**	**21**	0	<0.001	**-1.00**	**16**	0	<0.001	**-1.00**
Rodolphe	M	11	4	0.059	-0.47	**16**	4	0.015	-0.60	**15**	3	0.004	-0.67	3	**17**	0.001	0.70	4	**12**	0.038	0.50
Sestarde	F	1	**9**	0.011	0.80	0	**14**	<0.001	**1.00**	0	**22**	<0.001	**1.00**	0	**20**	<0.001	**1.00**	0	**10**	0.001	**1.00**
Toti	M	3	7	0.172	0.40	9	13	0.262	0.18	4	10	0.090	0.43	0	**20**	<0.001	**1.00**	11	8	0.324	-0.16
Tulie	F	**9**	2	0.033	-0.64	7	11	0.240	0.22	13	17	0.292	0.13	11	13	0.419	0.08	7	2	0.090	-0.56
Ubu	M	**12**	4	0.038	-0.50	**21**	0	<0.001	**-1.00**	**21**	0	<0.001	**-1.00**	**18**	2	<0.001	-0.80	**19**	0	<0.001	**-1.00**
Uranus	M	**14**	0	<0.001	**-1.00**	**19**	0	<0.001	**-1.00**	**13**	0	<0.001	**-1.00**	**12**	0	<0.001	**-1.00**	**8**	0	0.004	**-1.00**
Handedness category																					
LH-RH		4	5			6	5			5	5			3	7			3	6		
LAT				9				11				10				10				9	
EXC					5				6				8				8				8

Sex: *M* male, *F* female. Main columns: *LH* number of left-handed responses, *RH* number of right-handed responses, *B test* p-value of the binomial test performed on the number of right-handed and left-handed responses (when the test is significant the higher value is in bold), *HI* handedness index (bold characters indicate exclusive hand preference). Handedness category: *LH-RH* number of left-handed and right-handed baboons, *LAT* number of lateralized baboons irrespective of the direction of laterality, *EXC* number of exclusive right-handed and left-handed baboons (HI = 1 or HI = -1).

Captions

Figure 1. Experimental set-up of (a) the grasping task and (b) the food-begging task

Figure 2. Mean percentages (± SEM) of right-hand use for each task in the five positions. LL: extreme left, L: left, C: central, R: right, RR: extreme right. Significant interactions between tasks and positions are noted by asterisks, Wald tests *** $p < 0.001$.

Figure 3. Mean Handedness Indices (± SEM) for each task in the five positions. LL: extreme left, L: left, C: central, R: right, RR: extreme right. Significant correlations of individual HI values between tasks are noted by an asterisk, Spearman correlation coefficient * $p < 0.05$.

Figure 4. Mean absolute values of HI (± SEM) for each task in the five positions. LL: extreme left, L: left, C: central, R: right, RR: extreme right. Asterisks indicate significant variations of ABSHI across positions (Friedman analysis of variance *** $p < 0.001$) and between tasks (one-sample permutation test, (a) $p < 0.05$).

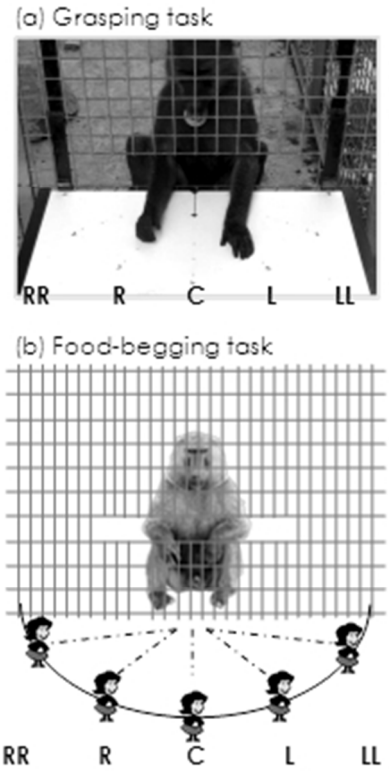

Figure 1
21x33mm (300 x 300 DPI)

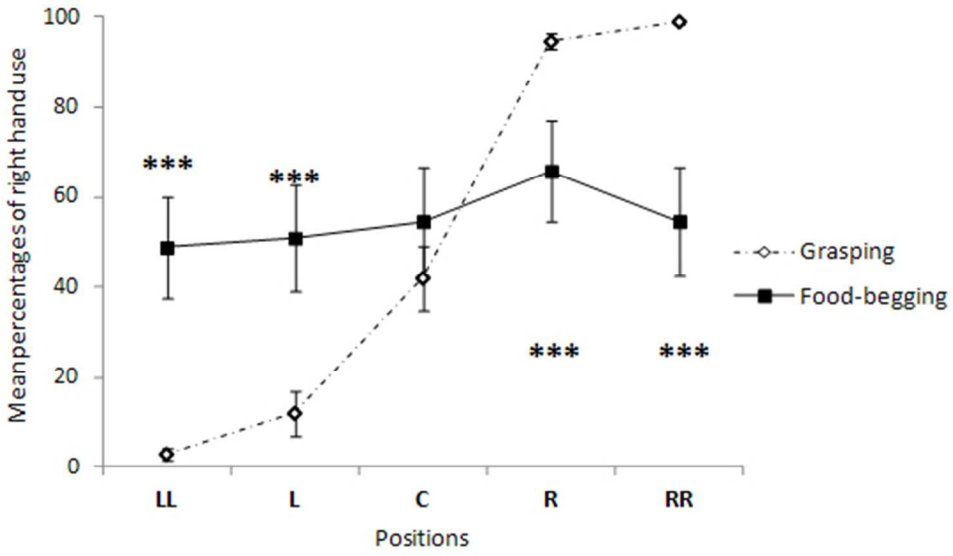

Figure 2
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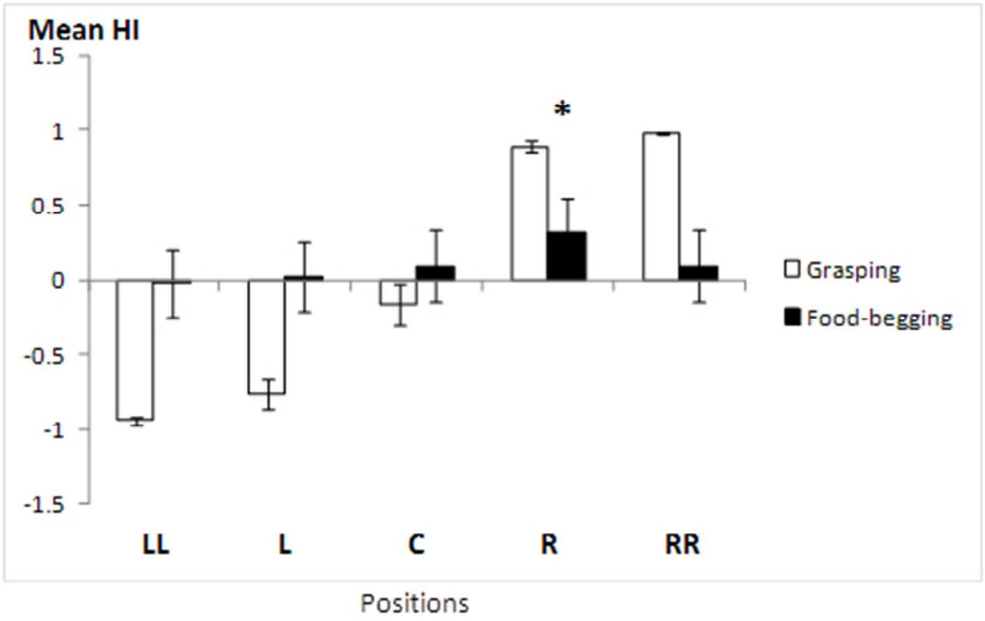

Figure 3
41x27mm (300 x 300 DPI)

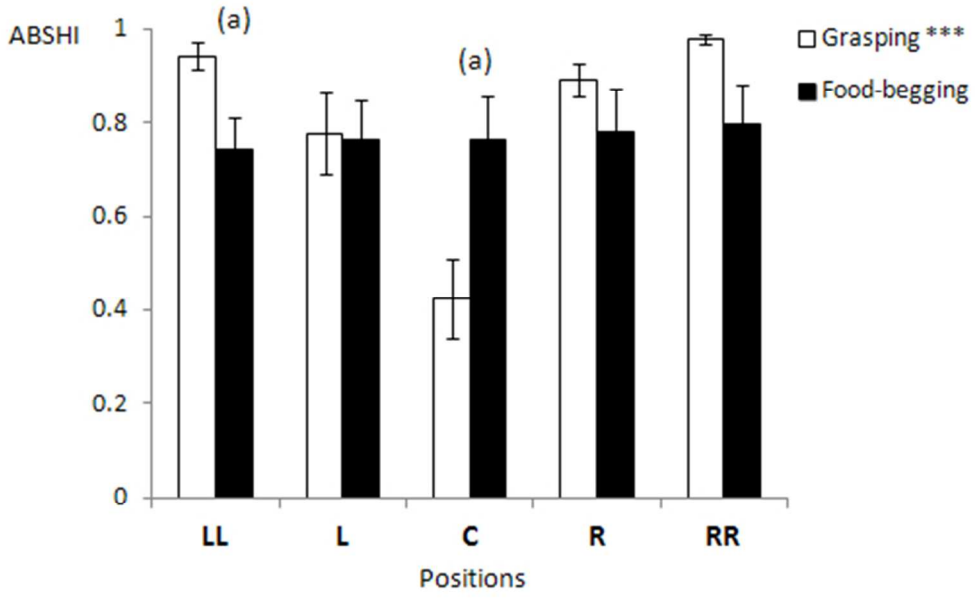

Figure 4. Mean absolute values of HI (± SEM) for each task in the five positions. LL: extreme left, L: left, C: central, R: right, RR: extreme right. Asterisks indicate significant variations of ABSHI across positions (Friedman analysis of variance *** $p < 0.001$) and between tasks (one-sample permutation test, (a) $p < 0.05$).
181x112mm (72 x 72 DPI)